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Studies on the ontogeny of *Streptopelia senegalensis aegyptiaca* (Latham, 1790)

3-Description of the optimum stage of the chondrocranium: Total body length of embryo: 53 mm

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Ethmoid region

Abstract The lordosis of the basal plate, previously observed in the younger stages, is no more evident. The anterior enlargement of the basicranial fenestra has restricted the acrochordal cartilage. The tectum in the present study is called the tectum posterius since it is purely of occipital origin. The metotic cartilage is provided by antero-ventral and posterior processes. Resorption of the antero-dorsal border of the acrochordal plate enlarges the size of the hypophyseal fenestra.

The parietotectal cartilage of the anterior half of the nasal capsule is continuous laterally as the paries lateralis nasi. The atrioturbinal cartilage is an outgrowth from the parietotectal cartilage. The maxilloturbinal cartilage develops from the ventro-lateral border of the posterior half of the parietotectal cartilage. The concha nasalis is deep and well formed.

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Introduction

A detailed account of the chondrocranium of *Anas* was presented by de Beer and Barrington (1934). Also definitive results were adduced by Engelbrecht (1958), May (1961), Müller

(1961) and Macke (1969) in the study of the avian chondrocranium. Mokhtar (1975) has presented a comprehensive study on the chondrocrania of *Upupa* and *Merops* (order coraciiformes). Also, Zaher and Abdeen (1991) and Zaher et al. (1991, 1993) presented detailed studies on the development of the neurocrania of *Corvus* and *Passer* (Passeriformes) and *Charadrius* (Charadriiformes) respectively.

Abd El-Hady and Zaher (1996), Abu Taira (1996a,b, 1997a,b), Abd El-Hady (2008a,b,c) and Zaher and Riad (2009, 2012) as well as El-Shikha (2011) studied the chondrocrania of *Corvus*, *Gallinula*, *Bubulcus*, *Coturnix*, *Streptopelia* and *Columba* respectively.

In spite of the extensive studies that had been presented on the development of the avian chondrocranium still, however, advantageous works are to be done in the subject.

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Nomenclature

- A.L. RE. S. T. aperture lateralis recessus scalae tympani
 A. M. RE. S. T. aperture medialis recessus scalae tympani
 A. SC. anterior semicircular canal
 ACR. C. acrochordal cartilage
 AD. CN. aditus conchae
 AN. P. PAR. N. anterior process of paries lateralis nasi
 AN. TYM. RE. anterior tympanic recess
 ANT. ORB. C. anterior orbital cartilage
 B. G. PT. C. backgrowing parietotectal cartilage
 B. V. blood vessel
 BAS. PL. basal plate
 BR. brain
 C. RDG. thick cartilaginous ridge of the backgrowing roof of the parietotectal cartilage and its anterior latero-dorsal process
 C. SANG. concavity lodging the supra-angular
 CAR. BRG. procartilaginous bridge
 CAR. CRS. cartilaginous crest of the processus oticus of the quadrate
 CAR. PRJ. cartilaginous projection supporting the sphenopalatine nerve
 CAR. RDG. the anterior cartilaginous ridge of the dorsal border of the metotic cartilage
 CAV. CN. cavum conchale
 CAV. MET. cavum metoticum
 CN. NAS. concha nasalis
 COL. SH. columellar shaft
 COM. EXOCPS. commissura exoccipitocapsularis
 COM. ORB. CAPS. commissura orbitocapsularis
 COM. PRV. commissura praevagalis
 COM. SOCPS. commissura supraoccipitocapsularis
 CON. ART. TU. & PAR. N. connection between atrio-turbinal cartilage and paries lateralis nasi
 CON. PAR. N. & MAX. TU. C. connection between the paries lateralis nasi and the maxilloturbinal cartilage
 CON. P. NAS. & PL. AN. blastematous connection between the postero-dorsal edge of the paranasal cartilage and the planum antorbitale
 CON. PT. C. & P. NAS. connection between parietotectal and the paranasal cartilage
 CONV. Q.J. concavity lodging the quadratojugal
 CRS. PA. crista parotica
 D. EN. ductus endolymphaticus
 EPBR. epibranchial
 F. SOCPS. fissure supraoccipitocapsularis
 FEN. NA. fenestra narina
 FEN. OLF. EV. fenestra olfactorium evehens
 FEN. SEP. INT. fenestra septi interorbitale
 FOR. B. V. foramen for the passage of a small blood vessel
 FOR. EN. foramen endolymphaticum
 FOR. LAT. CAR. lateral carotid foramen
 FOR. N. VI. posterior abducens foramen
 FOR. N. VII. foramen for the facial nerve
 FOR. OPTH. foramen for the ophthalmic artery
 FOR. PERI. foramen perilymphaticum
 FOR. PRO. foramen prooticum
 FOR. R. AMP. ANT. + UT. foramen for the ramus ampullaris anterior + utriculus
 FOR. R. AMP. POS. foramen for the ramus ampullaris posterior
 FOR. R. COCH. foramen for the ramus cochlearis
 FOR. R.M.N. foramen for the ramus nasalis medialis of the profundus nerve.
 FOR. R. SAC. foramen for the ramus sacculus
 FOR. Va. anterior foramen for the profundus nerve
 FOS. MET. fossa metotica
 FOS. SUB. fossa subarcuata
 FOS. SUP. COCH. fossa supracochlearis
 FR. frontal
 GAN. GEN. + ACCT. ganglion geniculatum + ganglion acousticus
 GAN. JUG. SUP. ganglion jugulare + ganglion superius
 GR. groove on the lateral wall of the cochlear portion
 GR. 1 a deep medio-dorsal groove in the anterior region of the parietotectal cartilage
 GR. 2 an extensive medio-dorsal concavity of the backgrowing roof of the parietotectal cartilage
 H. FOR. hypoglossal foramen
 IN. AU. M. internal auditory meatus
 INC. R. M. N. incisura for the ramus mandibularis nasi
 INF. CAR. COM. infracarotid commissure
 INF. TYM. RE. inferior tympanic recess
 L. SC. lateral semicircular canal
 M. C. meckel's cartilage
 MAX. TU. C. maxilloturbinal cartilage
 MET. C. metotic cartilage
 N. notochord
 NT. B.V. notch for the passage of a blood vessel
 O. A. occipital arch
 O.C. occipital condyle
 OL. N. olfactory nerve
 OPT. INC. incisura optica
 ORB. NAS. F. orbitonasal fissure
 P. EXCOL. processus extracolumellaris
 P. INCOL. processus infracolumellaris
 P. LAT. processus lateralis of the quadrate
 P. MAN. IN. processus mandibularis internus
 P. MED. medial process of the quadrate for the articulation with the pterygoid bone
 P. MET. C. V. antero-ventral process of metotic cartilage
 P. MX. AN. processus maxillaris anterior
 P. MX. P. processus maxillaris posterior
 P. ORB. processus orbitalis
 P. OT. processus oticus
 P. PARASEP. P. processus paraseptalis posterior
 P. PAROCPT. processus parietooccipitalis
 P. RT. processus retroarticularis
 P. SCOL. LAT. processus supracolumellaris lateralis
 P. SCOL. MED. processus supracolumellaris medialis
 P. TEC. processus tectalis
 PAR. POL. parapolar cartilage
 PIL. ANT. pila antotica
 PIL. ANT. SP. pila antotica spuria

PL. AN.	planum antorbitale	RE. AMP. POS.	recessus ampullaris posterior
PL. S.	planum supraseptale	RE. S.T.	recessus scalae tympani
POL. C.	polar cartilage	S.C.T.	strand of dense connective tissue
POS. ORB. C.	posterior orbital cartilage	S.CAPS. C.	supracapsular cartilage
POS. SC.	posterior semicircular canal	S. INT.	interorbital septum
POSTPROF. P.	postprofundal process	S.N.	nasal septum
PREF. COM.	prefacial commissure	S. POL. C.	suprapolar cartilage
PRN. P.	prenasal process	S. T. M.	secondary tympanic membrane
PROM. AMP. A.	prominentia ampullaris anterior	S. TYM. RE.	superior tympanic recess
PROM. AMP. POS.	prominentia ampullaris posterior	SOL. N.	solum nasi
PROM. COCH.	prominentia cochlearis	SQ.	squamosal
PROM. SC. L.	prominentia semicircularis lateralis.	ST	stapes or foot plate of the columella auria
PROM. SC. P.	prominentia semicircularis posterior	STYH.	stylohyal
PROM. UT.	prominentia utriculus	T.C.	trabecula communis
PROMN.	promontorium	T.M.	tympanic membrane
PT. C.	parietotectal cartilage	T. POL. COMX.	trabecula-polar complex
R. COCH.	ramus cochlearis	TEC. POS.	tectum posterius
RE. AMP. A.	recessus ampullaris anterior	UT.	utriculus

Thereupon the present work was planned for the full description of the chondrocranium of an optimum stage (53 mm) of *Streptopelia*. The development of the viscerocranium will be published soon.

Materials and technique

A large number of eggs of *Streptopelia senegalensis* were collected from the nests, where the embryos were soon eliminated from the shells. Living healthy embryos were quickly put in aqueous Bouin's solution for 24–48 h according to the size of the embryo. This was followed by repeated wash with 70% alcohol for 5–6 days. The total body length (T.B.L.) of each embryo was estimated by measuring the length from the tip of the beak to the cloacal opening. Three embryos of a T.B.L. (53 mm.) were chosen for sectioning. After embedding in paraffin wax, the embryos were cut in serial transverse sections of 15 microns in thickness and then stained with Mallory's triple stain. Projection was carried out with a magnification of 30×. From the drawings of projection, a graphic reconstruction of the chondrocranium was accurately prepared.

Observations

The basal plate and occipital region

What is mainly peculiar for the basal plate of the optimum stage of *Streptopelia* is its exceptional shortening in relation to the whole chondrocranium. It now constitutes slightly more than 1/9 of the total length of the cartilaginous skull (Fig. 1, BAS. PL.). The basal plate is now well developed as a thick dorsally concave floor in the form of a shallow bowl suspended between the two auditory capsules (Fig. 1). It extends from the foramen magnum posteriorly to the hypophyseal fenestra anteriorly (Fig. 1, HYPO. FEN.). In an antero-posterior direction it inclines smoothly downwards in a gentle curve, denoting

that the mesocephalic flexure is less than before. Accordingly, the lordosis of the basal plate, previously observed in the younger stages, is no more evident. As a whole, the basal plate shows an enormous thickness specially in the condylar region, as well as a remarkable extension in all directions.

Seen dorsally, the basal plate (Fig. 1, BAS. PL.) is roughly triangular in shape. The broad base of the triangle is its posterior margin which is provided with the mid bulky mass that forms the ventral border of the foramen magnum i.e., the occipital condyle (Fig. 2, O.C.). The anterior apex of the triangle is the narrow acrochordal cartilage (Fig. 2, ACR. C.).

Just posterior to the acrochordal cartilage, and in the region of the previous lordosis, more resorption of pre-existing cartilage has increased the size of the basicranial fenestra specially its anterior portion (Figs. 1 and 2, BAS. FEN.). The anterior enlargement of the basicranial fenestra has restricted the acrochordal cartilage (ACR. C.) to a mere narrow cartilaginous strip separating the latter fenestra from the hypophyseal fenestra (Figs. 1 and 2, HYPO. FEN.).

Anteriorly, the notochord (N.) traverses freely the dorsal surface of the basicranial fenestra (Figs. 1 and 2, BAS. FEN.). Far anteriorly, it is embedded, but dorsally exposed, on the mid-dorsal surface of the acrochordal cartilage (Fig. 1, ACR. C.).

The occipital region is conservative in its structure and does not differ principally from the general avian fashion. The occipital arch (Figs. 1 and 2, O.A.) of the present stage has attained its full definitive form. The lateral border of its lower portion passes uninterruptedly sideways into the ventral border of the prominentia ampullaris posterior (Figs. 3 and 6, PROM. AMP. POS.) and prominentia semicircularis posterior (PORM. SC. P.) of the auditory capsule via the commissura exoccipitocapsularis (Figs. 3 and 6, COM. EXOCPS.).

What is peculiar in the optimum stage of *Streptopelia* is the mode of formation of the tectum synoticum plus posterius (TEC. POS.). It seems most probable that the tectum is mainly formed by the fusion of the two occipital arches. The auditory capsules seem to have the least share in its formation. They

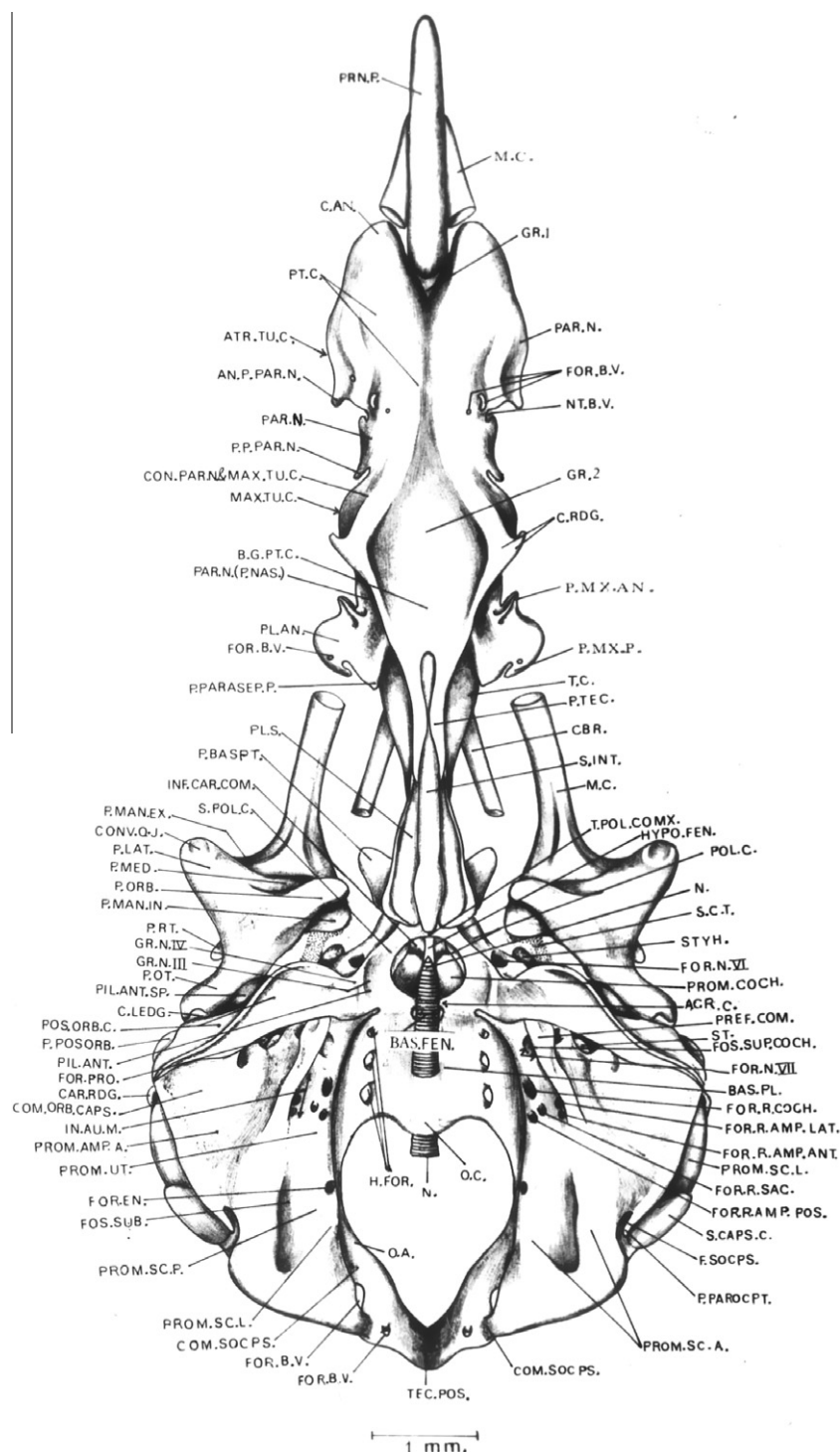


Figure. 1 Graphical reconstruction of the chondrocranium of optimum stage of *Streptopelia senegalensis* in a dorsal view.

only contribute with minimum lateral portions in its material. For this reason, the tectum in the present study is called the tectum synoticum plus posterius, or most preferably the tectum posterius since it is purely of the occipital origin (Figs. 1 and 2, TEC. POS.).

Of particular interest is the fact that the tectum posterius in *Streptopelia* lacks the processus anterior tecti found in *Pterocles*

(Mokhtar et al., 1983). It seems that *Pterocles* is the only described bird that possesses such a process. Its presence is a typical lacertilian character (El-Toubi and Kamal, 1959).

At the postero-lateral corner of the basal plate, the number of the hypoglossal foramina is rendered constant being three as previously mentioned in the early and intermediate stages of *Streptopelia*.

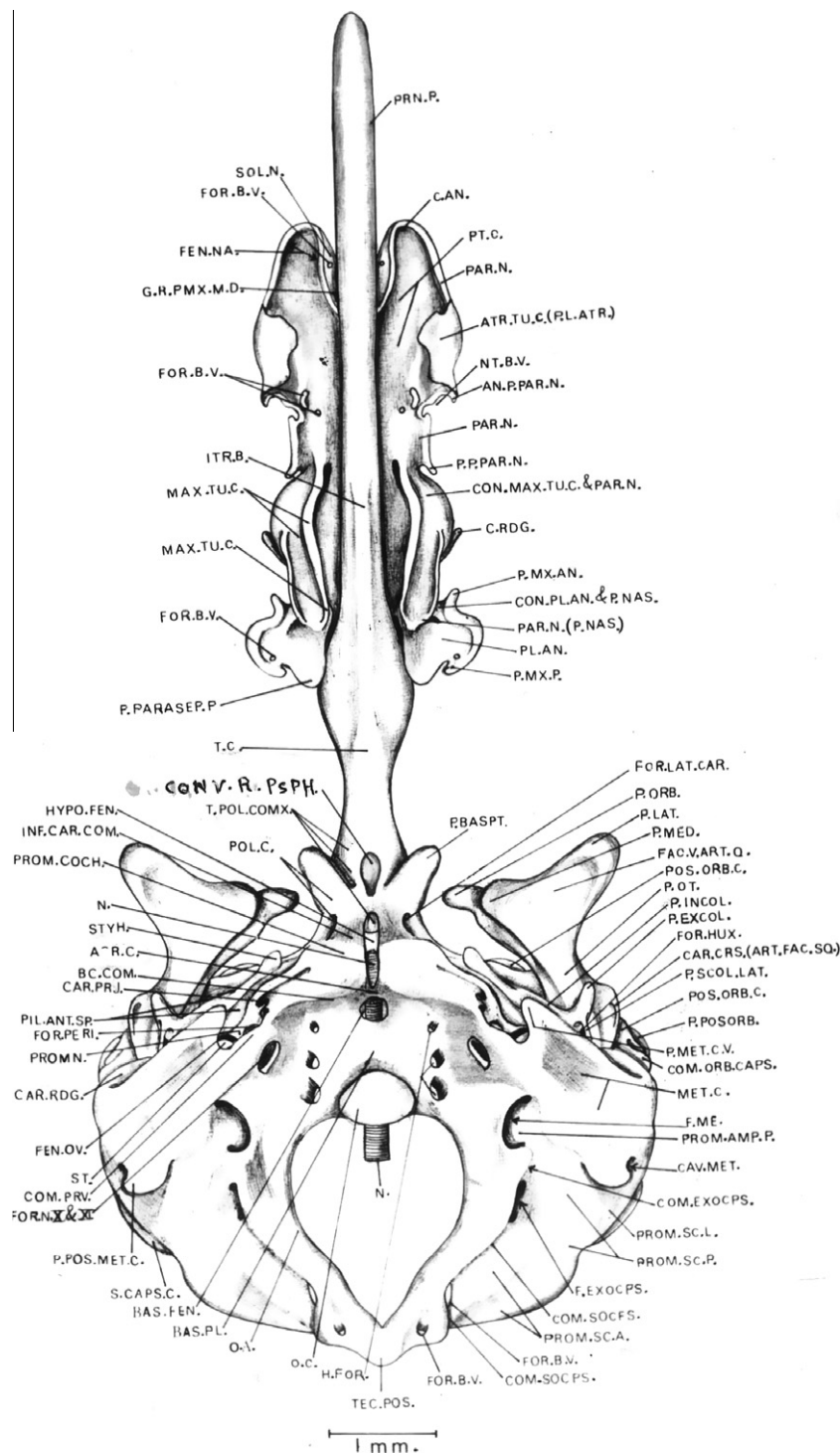


Figure. 2 Graphical reconstruction of the chondrocranium of optimum stage of *Streptopelia senegalensis* in a ventral view.

The auditory capsule

In the optimum stage of *Streptopelia*, the two auditory capsules are connected together dorsally by the tectum posterius (Fig. 1, TEC. POS.). The basicranial fenestra (Figs. 1 and 2, BAS. FEN.) represents the separating cavity between their two cochlear portions. The basicapsular commissure (BC. COM.), as well as the commissura praevagalis (COM. PRV.)

connect the auditory capsule with the lateral edge of the basal plate (Fig. 1, BAS. PL.). The lateral wall of the prominencia cochlearis (PROM. COCH.) is perforated by a dorsal fenestra ovalis (Fig. 3, FEN. OV.). A dorsal perilymphatic foramen is present below the fenestra ovalis and separated from it by the promontorium (Figs. 2 and 3, PROMN.).

The fossa subarcuata (FOS. SUB.) separates the prominencia semicircularis anterior (Fig. 1, PROM. SC. A.) from the

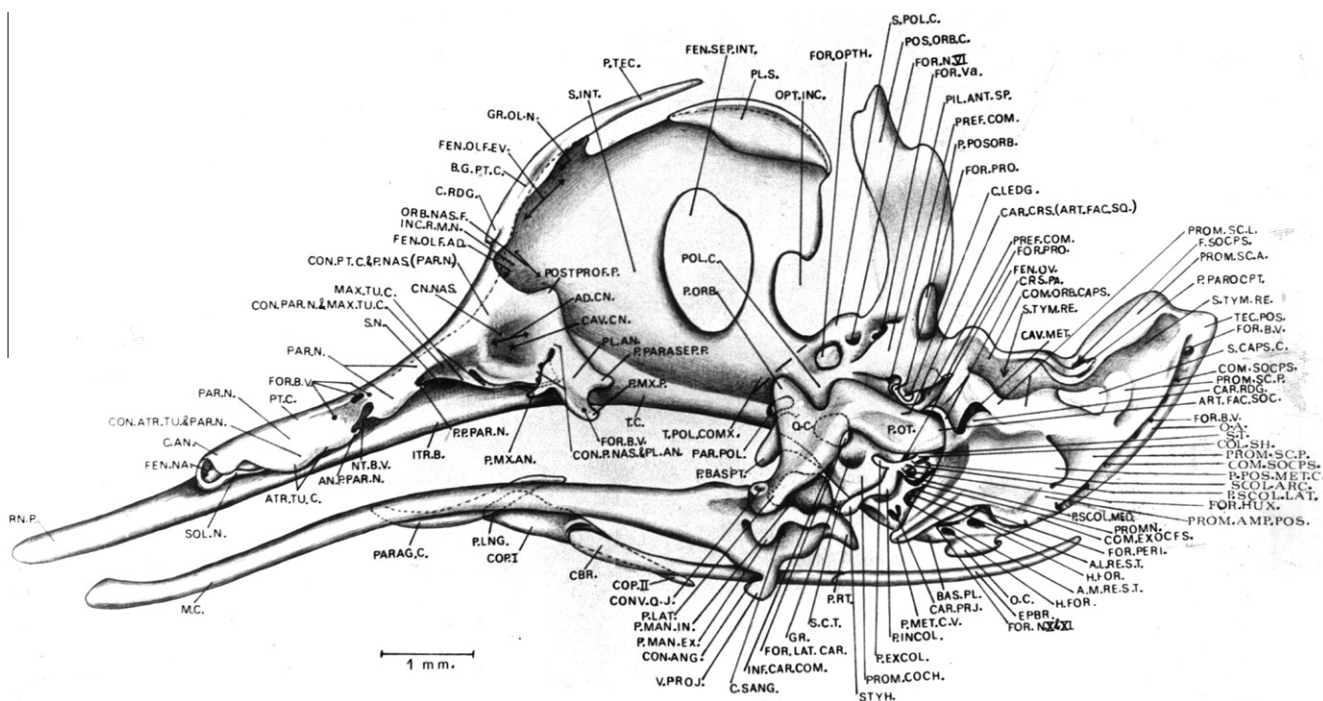


Figure 3 Graphical reconstruction of the chondrocranium of optimum stage of *Streptopelia senegalensis* in a lateral view.

prominentia semicircularis posterior (Fig. 1, PROM. SC. P.). The foramen endolymphaticum (Fig. 1, FOR. EN.) occupies the dorso-medial angle of the prominentia ampullaris posterior (PROM. AMP. POS.).

In this stage, the metotic cartilage is provided by antero-ventral and posterior processes (Fig. 2, P.MET. C.V. and P.POS.MET.C.). The lower portion of the metotic cartilage forms a continuous floor below the anterior two thirds of the canicular portion.

In the present stage of *Streptopelia*, a newly formed cartilaginous connection between the occipital arch (O.A.) and the auditory capsule is developed. Such a connection is the first indication of the formation of a commissura exoccipitocapsularis (Fig. 3, COM. EXOCPS.).

Of a particular interest in the optimum stage of *Streptopelia* is the development of two extra-cartilaginous elements related to the lateral wall of the canicular portion of the auditory capsule. These are the commissura parietooccipitalis and the supracapsular cartilage (Fig. 1, COM. PAROCPT. and S.CAPS. C.). The commissura parietooccipitalis represents the posterior extension of the commissura orbitocapsularis (Fig. 3, COM. ORB. CAPS.). The supracapsular cartilage (S. CAPS. C.) has an isolated center of chondrification, but in the present stage, it acquires close contact to the prominentia semicircularis lateralis (Fig. 3, PROM. SC. L.) but with a clear line of demarcation between them.

The orbital region

In the optimum stage of *Streptopelia*, the upgrowth of the interorbital septum reaches its maximum condition (Figs. 3 and 4, S. INT.). It is fenestrated by the fenestra septi interorbitalis (Figs. 3 and 4, FEN. SEP. INT.). The processus tectalis of the parietotectal cartilage (Fig. 3, P. TEC.) merges without any

boundary with the dorsal surface of the interorbital septum below it. The major portion of the preoptic root of the anterior orbital cartilage (Fig. 2, ANT. ORB. C.) is completely regressed.

What remains of the anterior orbital cartilage is the thoroughly chondrified planum supraseptale (Fig. 3, PLAN. SUP.). An oval fenestra septi interorbitalis (Figs. 1 and 2 Figs. 3 and 4, FEN. SEP. INT.) has been formed in the central portion of the interorbital septum (S. INT.) by a process of resorption of the pre-existing cartilage.

With the resorption of the antero-dorsal border of the acrochordal plate (Figs. 1 and 2, ACR. C.), the size of the hypophyseal fenestra is enlarged (Fig. 1, HYPO. FEN.).

Resorption also affects the dorsal surface of the suprapolar cartilage which becomes now more reduced in size (Fig. 1 S. POL. C.). The ophthalmic foramen is relatively enlarged than before. The pila antotica spuria (Fig. 3, PIL. ANT. SP.) becomes thicker and attached to the antero-lateral surface of the posterior orbital cartilage (Fig. 3, POS. ORB. C.).

In the present stage, the front border of the posterior orbital cartilage and the dorsal side of the pila antotica (Fig. 3, PIL. ANT.) are further regressed.

The postorbital process of the posterior orbital cartilage (Fig. 3, P.POS. ORB.) increases in length and is heavily chondrified.

In the optimum stage of *Streptopelia*, the distal tips of the processus orbitocapsularis (P. ORB. CAPS.) and processus prooticus (P. PR.) form together a commissura orbitocapsularis (Figs. 3 and 5, COM. ORB. CAPS.).

The ethmoid region

In the optimum stage of *Streptopelia*, the prenasal process (Figs. 1–3, PRN.P.) has extended further anteriorly and is af-

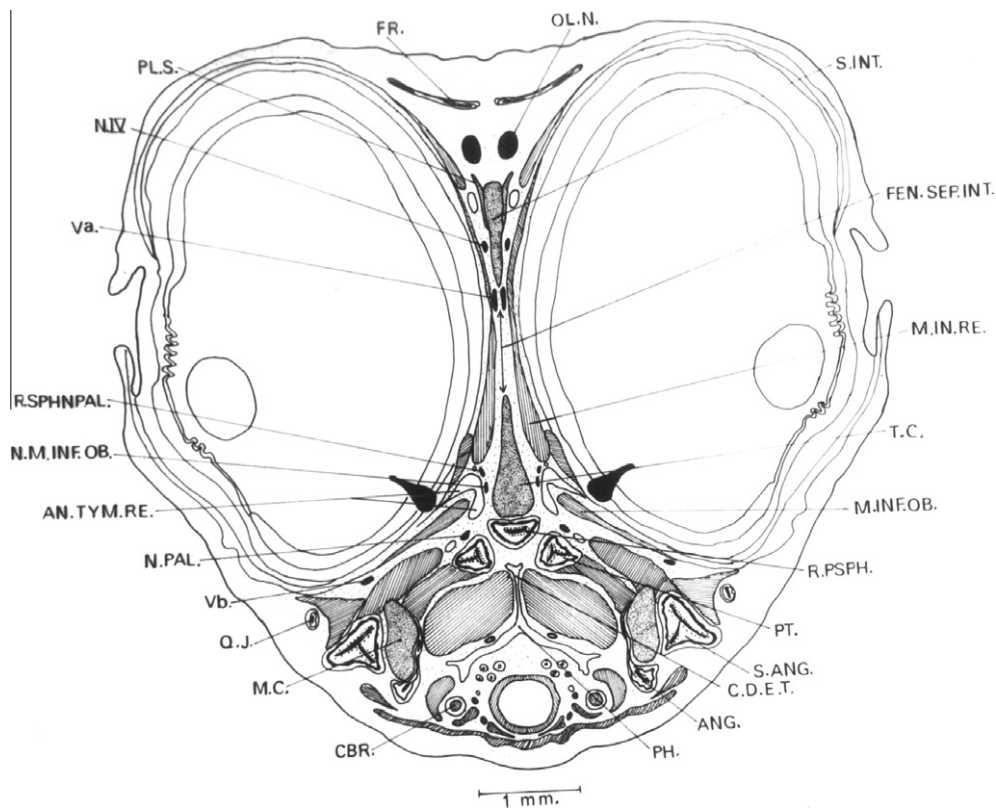


Figure. 4 Transverse section passing through the interorbital region of the optimum stage of *Streptopelia*.

affected by the resorption process along its antero-dorsal border. The two cone-shaped cupulae anteriores (Figs. 1 and 2, C. AN.) form the anterior part of the nasal capsule. The parietotectal cartilage (PT. C.) of the anterior half of the nasal capsule is continuous laterally as the paries lateralis nasi (Figs. 1 and 2, PAR. N.). The posterior half of this paries lateralis has further developed downwards, and its postero-lateral process (P.P. PAR. N.) covers laterally the postero-ventral extremity of the atrioturbinal cartilage (Figs. 2 and 3, ATR. TU. C.).

The atrioturbinal cartilage is an outgrowth from the parietotectal cartilage (PT. C.) and its position marks the virtual line of separation between the tectum nasi and its paries lateralis nasi (Fig. 3, PAR. N.).

The maxilloturbinal cartilage (Fig. 3, MAX. TU. C.) develops from the ventro-lateral border of the posterior half of the parietotectal cartilage (Fig. 3, PT. C.). Its ventral border forms a horizontal shelf which should be considered as its medially directed secondary lamella. A connection has been achieved between the maxilloturbinal and the paranasal cartilages (Figs. 2 and 3, CON. MAX. TU. and PAR. N.).

The parietotectal cartilage (Fig. 3, PT. C.) extends posteriorly to form the roof of the posterior part of the nasal capsule. More posteriorly, the connection between the interorbital septum (S. INT.) and the parietotectal cartilage is lost and the latter ends as a processus tectalis (Fig. 3, P. TEC.).

In the present stage of *Streptopelia*, the planum antorbitale (Fig. 3, PL. AN.) loses its connection with the paries lateralis nasi and the paranasal cartilage (PAR. N.). Only the processes paraseptalis posterior (Fig. 3, P. PARASEP. P.) is present. With the exaggerated elongation of the backgrowing parietotectal cartilage, the post-profunda commissure is

broken and a postprofunda process (Fig. 3, POSTPROF. P.) is formed.

The concha nasalis (Figs. 2 and 3, CN. NAS.) is deep and well formed. The cavum conchale (CAV. CN.) is triangular in shape with the base of the triangle directed posteriorly.

In this stage, the solum nasi (Figs. 2 and 3, SOL. N.) is anteriorly reduced. It is only represented as a small process coming back from the cupola anterior (Figs. 2 and 3, C. AN.).

Discussion

The basal plate

In *Streptopelia*, the basal plate constitutes slightly more than 1/9 of the total length of the cartilaginous skull; this exaggerated condition not observed in the previous works except in *Merops* (Mokhtar, 1975) and *Pterocles* (Mokhtar et al., 1983).

The present study shows that in the posterior occipital region the notochord tends gradually to have a central position although somehow cerebral. This condition seems to coincide with what is described for *Pyromelana* (Engelbrecht, 1958) and *Pterocles* (Mokhtar et al., 1983). However in the avian literature there is an agreement that the notochord in the optimum stage is covered dorsally during development throughout its major portion and its course is traced by the remarkable mid-dorsal elevation (Anas, De Beer and Barrington, 1934, *Spheniscus*; Crompton, 1953; *Upupa* and *Merops*; Mokhtar, 1975).

In *Streptopelia*, there is no evidence for the formation of paired centers of a tectum synoticum originating from the auditory capsules similar to the condition prescribed in

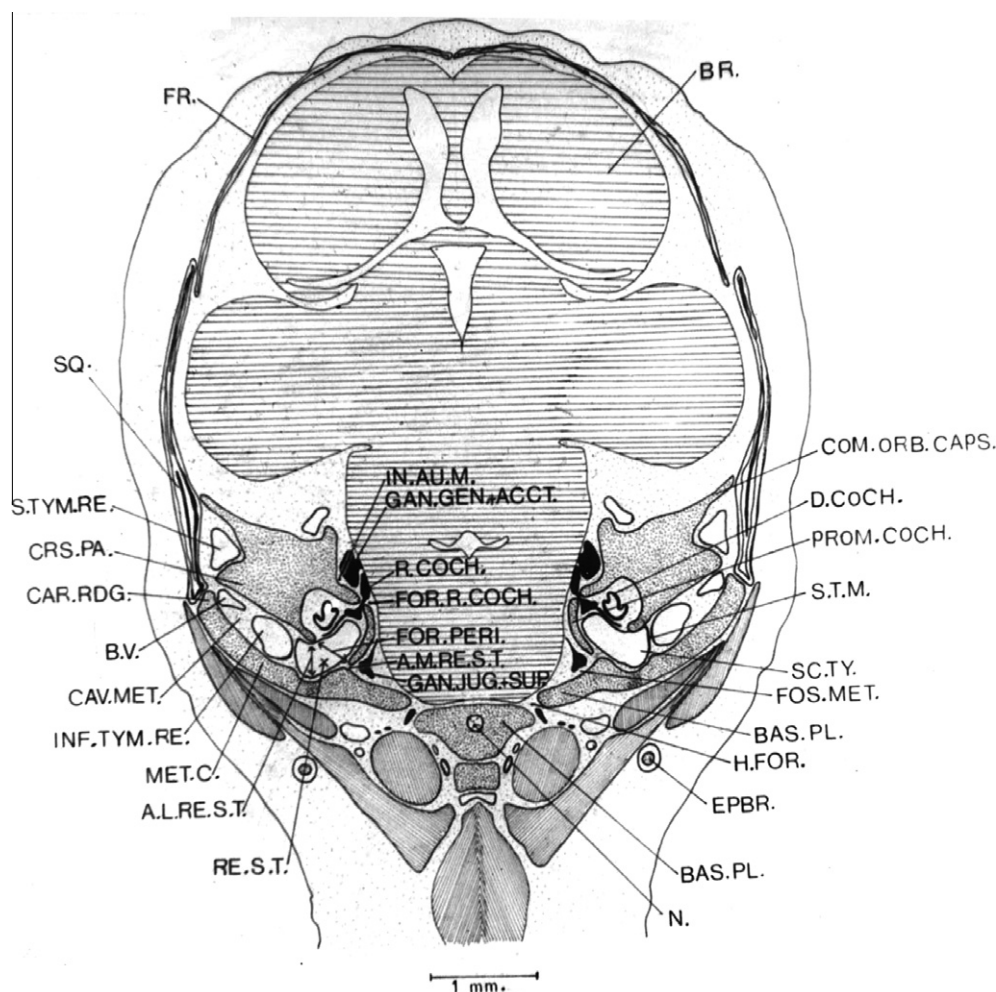


Figure 5 Transverse section passing through the auditory region of optimum stage of *Streptopelia senegalensis*.

Pyromelana (Engelbrecht, 1958), *Upupa* & *Merops* (Mokhtar, 1975), *Pterocles* (Mokhtar et al., 1983), *Gallinula* and *Bubulcus* (Abu Taira, 1996b, 1997a). As far as the authors are aware, the foramina of the tectum posterior seem unique in *Streptopelia* and have never been mentioned in any described bird.

In *Streptopelia*, as in the other investigated birds the occipital region is essentially an inverted heart shaped frame around the foramen magnum. However, in *Pterocles* (Mokhtar et al., 1983) the foramen magnum is oval shaped similar to the condition found in *Rhea* (Müller, 1961).

In *Streptopelia*, the foramen magnum faces posteriorly and ventrally as commonly found in birds.

Of particular interest is the fact that the tectum posterius in *Streptopelia* lacks the processus anterior tecti, however, such a process is found in *pterocles* (Mokhtar et al., 1983). It seems that *pterocles* is the only described bird that possesses such a process. Its presence is a typical lacertilian character (El-Toubi and Kamal, 1959).

The absence of a connection between the lateral border of the occipital arch behind the commissura exoccipitocapsularis and the metotic cartilage is also observed in *Merops* (Mokhtar, 1975) and *pterocles* (Mokhtar et al., 1983). However in the other described birds, the fusion between the occipital arch and the metotic cartilage is variably extended.

In *Streptopelia* the basicranial fenestra appears only in the present stage, and not before by resorption of cartilage. This agrees with the studies on *Tinnunculus* (Suschkin, 1899), *Pyromelana* (Engelbrecht, 1958), *Upupa* and *Merops* (Mokhtar, 1975), *Pterocles* (Mokhtar et al., 1983), *Gallinula*, and *Bubulcus* (Abu-Taira, 1996b, 1997a). On the other hand, such a fenestra, is not represented in the basal plate of *Emu* (Lutz, 1942), *Ostrich* (Frank, 1954), *Fulica* (Til Macke, 1969) and *Bubulcus* (Abu-Taira, 1997a).

The absence of the basicranial fenestra in the early developmental stages of some birds coincides with that of *Urodela*, *Anura*, *Lacertilia* and *Crocodylia* (De Beer, 1937). The lack of this fenestra in other birds, either in early or all ontogenetic stages, is thus, considered as a primitive phylogenetic character.

The auditory region

The present study shows that the fenestra ovalis develops by resorption in the pre-existing cartilage. This is the condition of most described birds. However, Sonies (1907) considers the fenestra ovalis as a remnant of the cochleocanicular fissure, while from De Beer's description (1937), it is not clear as whether it develops from the cochlear or the canicular portions.

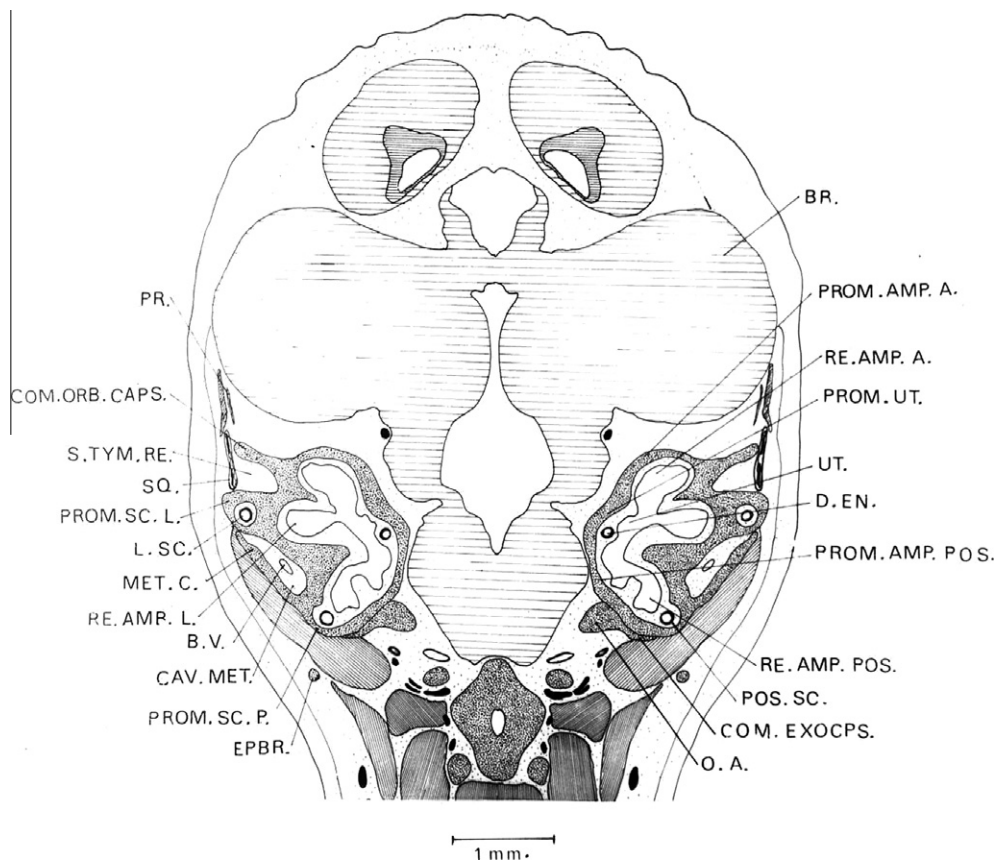


Figure. 6 Transverse section passing through the auditory region of optimum stage of *Streptopelia senegalensis* showing the nature of commissura exoccipitocapsularis.

The prefacial commissure has a general occurrence among almost all sauropsidan forms. In birds, the distinct position of the commissure slightly varies from one form to another. In *Anas* (De Beer and Barrington, 1934), *Struthio* and *Nyctisyrignus* (Frank, 1954), *pyromelana* (Engelbrecht, 1958) as well as in *Merops* (Mokhtar, 1975), the prefacial commissure connects both portions of the auditory capsules in young stages. In older embryos, the above mentioned commissure extends to fuse with the lateral edge of the basal plate. In *Rhea* (Müller, 1961) and *Fulica* (Macke, 1969), it extends up to the acrochordal cartilage and joins the posterior border of the hypoglossal foramen. In *Charadrius* (Zaher and Abdeen, 1991), it shows no relation to the basal auditory capsule between the cochlear and canicular portions. This is similar to the condition of *Upupa* and *Merops* (Mokhtar, 1975) and *Pterocles* (Mokhtar et al., 1983).

In birds, the series of commissures connecting the auditory capsule with the surrounding cartilaginous structures are: the basicapsular commissure, the commissura exoccipitocapsularis and the commissura supraoccipitocapsularis. Müller (1961) is the first to draw the attention that a straight analogy is present between these two latter commissures in mammals. Other than these commissures, a commissura parietooccipitalis or a processus parietooccipitalis have a common occurrence in birds. These are first designated by Müller (1961) from analogous structures present in mammals. In the present study, the commissura parietooccipitalis runs aside and is separated from the prominentia semicircularis anterior with an elongated narrow

slit representing the fissura supraoccipitocapsularis as in *Rhea* (Müller, 1961). On the other hand, the latter fissure is absent in *Fulica* (Macke, 1969), *Upupa* (Mokhtar, 1975) and *Pterocles* (Mokhtar et al., 1983).

The orbital region

In the present study, the interorbital septum is fenestrated by a fenestra septi interorbitalis, a condition present in many described birds e.g. *Spheniscus* (Crompton, 1953), *Pyromelana* (Engelbrecht, 1958), *Rhea* (Müller, 1961), *Fulica* (Macke, 1969), *Merops* (Mokhtar, 1975). In *Anas* (De Beer and Barrington, 1934), two fenestrae septi interorbitalis are present. On the other hand, in *Upupa* (Mokhtar, 1975), the fenestra septi interorbitalis is absent.

In *Streptopelia* as commonly found in birds, the anterior orbital cartilage undergoes a very rapid regression and what will remain represents the planum suprasedale. It is represented in the majority of birds as *Anas* (De Beer and Barrington, 1934), *Spheniscus* (Crompton, 1953), *Struthio* (Frank, 1954), *Rhea* (Müller, 1961), *Fulica* (Macke, 1969), *Pterocles* (Mokhtar et al., 1983) as well as *Charadrius* (Zaher and Abdeen, 1991). However, in *Pyromelana* (Engelbrecht, 1958) and *Upupa* (Mokhtar, 1975), the resorption of the anterior orbital cartilage, which happens in late ontogenetic stages, involves the whole structure and no corresponding planum suprasedale is thus left although the skull here is also tropicbasal.

In all investigated birds, the orbital and auditory regions are connected together by commissura orbitocapsularis. In *Streptopelia*, as well as in the majority of birds, it is formed when the posterior orbital cartilage comes to fuse to the processus oticus. The two processes have a simultaneous late appearance. In *Pyromelana* (Engelbrecht, 1958) and *Rhea* (Müller, 1961), the processus prooticus has a prior appearance. In *Fulica* (Macke, 1969), the reverse is true similar to the condition of *Merops* (Mokhtar, 1975). In *Spheniscus* (Crompton, 1953), Ostrich (Frank, 1954) and *Upupa* (Mokhtar, 1975), the commissura orbitocapsularis is formed out of the processus orbitocapsularis which realizes an intimate connection with the auditory capsule with the intervention of a processus prooticus.

The presence of a cartilaginous postorbital process is a common feature for the avian skull. It is present in *Streptopelia* as well as in *Tinnunculus* (Suschkin, 1899), *Anas* (De Beer and Barrington, 1934), *Pyromelana* (Engelbrecht, 1958), *Strix* (May, 1961), *Rehea* (Müller, 1961), *Fulica* and *Gallinula* (Macke, 1969) *Upupa* and *Merops* (Mokhtar, 1975), *Pterocles* (Mokhtar et al., 1990), *Charadrius* (Zaher and Abdeen, 1991), *Coturnix* (Abd El-Hady, 2008c), *Gallinula* (Abu-Taira, 1996b), *Bubulcus* (Abu-Taira, 1997a) and *Columba* (El-Shikha, 2011). In *Struthio* (Frank, 1954) and *Spheniscus* (Crompton, 1953), the cartilaginous postorbital process is lacking.

The ethmoid region

In the present study, the prenasal process does not show any sign of ossification but undergoes resorption. It represents an anterior extension of the intertrabecular bar. This is similar to the condition present in *Upupa* and *Merops* (Mokhtar, 1975), *Passer* and *Pterocles* (Mokhtar et al., 1983). This contradicts with what seems to be prevalent in the avian literature that the process grows out of the trabecula communis, as in *Phalacrocorax* (Slaby, 1951), *Spheniscus* (Crompton, 1953), Ostrich (Frank, 1954), *Pyromelana* (Engelbrecht, 1958) *Rhea* (Müller, 1961), *Charadrius* (Zaher and Abdeen, 1991), *Coturnix* (Abd El-Hady, 2008c), *Gallinula* (Abu-Taira, 1996b), *Bubulcus* (Abu-Taira, 1997a) and *Columba* (El-Shikha, 2011). In *Anas* (De Beer and Barrington, 1934), the prenasal process is the anterior prolongation of the nasal septum.

Engelbrecht (1958) is the first to draw the attention that in all birds, a thickened intertrabecular bar in the ethmoid region is a characteristic feature. This is confirmed by the findings of Zaher and Abdeen (1991) in *Charadrius*, Abu-Taira (1996a,b) in *Gallinula*, Abd El-Hady (2008c) in *Coturnix* and El-Shikha (2011) in *Columba*.

An atrioturbinal cartilage is always developed in birds. An exception, is the condition observed in *Streptopelia* as well as in *Charadrius* where it forms a simple ledge. In *Anas* (De Beer and Barrington, 1934) *Struthio* (Frank, 1954), *Spheniscus* (Crompton, 1953), *Pyromelana* (Engelbrecht, 1958) *Rhea* (Müller, 1961) and *Upupa* (Mokhtar, 1975), secondary lamellae are present. A further complication in the structure of the atrioturbinal cartilage is observed in *Merops* (Mokhtar, 1975), where tertiary lamellae are developed.

In the present species, the concha nasalis represents the dorsal component of the paranasal cartilage. However, in *Pyromelana* (Engelbrecht, 1958), the concha nasalis is totally absent. In *Streptopelia*, as commonly found in birds, the con-

cha nasalis is of the simplified type due to the absence of the extraconchal recess (Zaher and Abdeen, 1991 in *Charadrius*; Abu-Taira (1996a,b) in *Gallinula*; Abd El-Hady, 2008c in *Coturnix* and El-Shikha, 2011 in *Columba*). An exception to this is the condition of *Fulica* (Macke, 1969), where a postconchal recess is present.

In *Streptopelia* the simple primary lamella of the maxilloturbinal cartilage carries a secondary lamella. Such a condition is also represented in *Pyromelana* (Engelbrecht, 1958), *Upupa* (Mokhtar, 1975) and *Pterocles* (Mokhtar et al. (1983), *Charadrius* (Zaher and Abdeen, 1991) and *Coturnix* (Abd El-Hady, 2008c). In *Anas* (De Beer and Barrington, 1934), *Fulica* (Macke, 1969), and *Rhea* (Müller, 1961), the maxilloturbinal cartilage is represented by an unbranched cartilaginous lamella which rolled up laterally in the form of a spiral. A more complicated maxilloturbinal lamella is found in the Ostrich (Frank, 1954), where its secondary lamella curls dorsally forming semicircular structures.

In the present study, as commonly found in the neurocranium of the described birds, the planum antorbitale forms the posterior and the postero-lateral walls of the nasal capsule. Thus, it is homologous with the lamina orbitonasalis of other forms such as *Scyllium*, *Lacerta* and *Lepus* (De Beer, 1937). In *Streptopelia* as well as in *Charadrius* (Zaher and Abdeen, 1991), the planum antorbitale extends in a vertical manner, while in *Rhea* (Müller, 1961) and *Pterocles* (Mokhtar et al., 1983), it assumes a horizontal position below the eyes. In *Streptopelia*, the planum antorbitale has only a processus maxillaries posterior, while the processus maxillaries anterior is absent. Such a condition is similar to what is found in *Spheniscus* (Crompton, 1953), Ostrich (Frank, 1954), *Upupa* (Mokhtar, 1975) and *Charadrius* (Zaher and Abdeen, 1991). Both processes are not frequently met with among the described birds except in *Rhea* (Müller, 1961). The presence of these two processes is also commonly found in squamate reptiles (De Beer, 1937).

In *Streptopelia* as well as in most described birds, the lamina transversalis anterior represents the floor of the nasal capsule in the transitional area between the nasal vestibule and the main nasal cavity. Parker (1891a,b) described it as a plate turned inwards ventrally from the ectethmoid and against the mesethmoid. However, Frank (1954) and Engelbrecht (1958) called it the median extension of the common posterior end of the lateral wall and the atrioturbinal cartilage. Müller (1961) was the first to homologize such a median extension in *Rhea* with the lamina transversalis anterior of reptiles which have the same topography but of a different origin.

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